CHEMICAL DEFENSE AND SOUND PRODUCTION IN AUSTRALIAN TENEBRIONID BEETLES (*ADELIUM* SPP.)*

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Introduction

Girdled eucalyptus trees, felled to make room for grazing pasture, are a common sight in rural Australia. In the dead and decaying stumps that are strewn through the countryside, many insects flourish. Two of these, the congeneric tenebrionid beetles *Adelium percatum* and *A. pustulosum* (subfamily Adeliinae) possess interesting defense mechanisms that we here describe. Both have eversible abdominal glands such as are commonly found in Tenebrionidae (Roth, 1945), but some features of the chemistry and biology of the glands are anomalous. Moreover, *A. pustulosum* has a stridulatory apparatus that may function for acoustical reinforcement of the chemical defense.

Materials and Methods

Both species of *Adelium* are black and, lacking hindwings, are flightless. Several dozen specimens were taken singly and in small groups in and under pieces of decaying eucalyptus wood in sheep pasture near Gudgenby, Australian Capital Territory, in mid-April, 1973 (Fig. 2). They were maintained in plastic containers, and given water, sucrose, and a variety of cereal-based foods. Initial behavioral and electronmicroscopic studies were done at the laboratories of the Division of Entomology, C. S. I. R. O., Canberra, where T. E. and M. E. were guests. Secretion was shipped to B. C. and J. M. for chemical analysis at the University of California, San Diego. Some beetles survived travel to Cornell, where acoustical studies were made by D. A., R. R. and T. E.

Scanning electronmicrographs were made with a JEOL (JSMU-UE) instrument. Preservation of beetles with everted glands was

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effected by first immersing them in cold (—195°C) liquid Freon (while held in forceps to cause eversion) and then transferring them to a tissue freeze-dryer for desiccation.

Instruments for chemical analyses included conventional gas chromatographs and an LKB-9000 gas chromatograph-mass spectrometer.

Sound recordings were made at 23-25°C with a condenser microphone from a Holgate Ultrasonic Receiver MK.V [frequency response ± 12 db from 1 to 100 kHz; sensitivity at preamplifier output 268 mv (rms)/μbar at 60 kHz (determined by substitution)], an Ithaco Amplifier Model 225 [variable amplification range from 0 to 80 db; flat frequency response (within 3 db) in range of 0.5 Hz to 100 kHz] and a Lockheed Magnetic Tape Recorder/Reproducer Model 419 [recording speed set at 30 inches/sec; flat frequency response (within 3 db) in range from 0.2 to 100 kHz; input sensitivity of 1.4 volt (1.0 volt rms) for ± 40% deviation]. Sound intensity was measured with a Brüell and Kjaer Precision Sound Level Meter Type 2203 and a Brüell and Kjar Condenser Microphone Cartridge Type 4145. The intensity measurements were limited to audio frequencies due to limitations in the frequency response of the Brüell and Kjaer Microphone [flat frequency response (within 2 db) in range from 2.6 Hz to 18.5 kHz].

Instruments used for displaying and recording temporal patterns of the sound included a Tektronix storage oscilloscope (Model 4103N) with differential amplifier (Model 5A22N) and Polaroid camera, and a Tektronix dual beam oscilloscope (Model 502A) with a Grass Kymograph camera (Model C4N). Timing marks were generated on the oscilloscope with a Hewlett-Packard function generator (Model 3310A).

Sound spectograms were made with a Kay Elemetrics Sonograph (Model 7029A). Low frequency background noise was filtered as needed during playback of the recordings with a Krohn-Hite filter (Model 3550).

Chemistry of the Secretion

It was clear from the outset that the secretion of both species was quinonoid in nature. The beetles responded typically to rough handling by protruding their glands, and the oily golden-brown fluid that visibly coated the everted structures had the unmistakable penetrating odor of benzoquinones, and the characteristic quinonoid

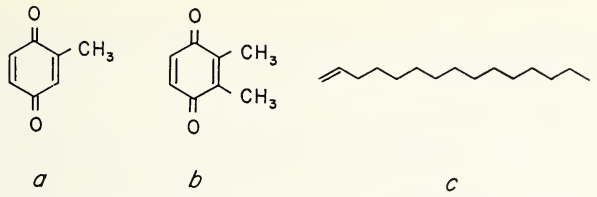

Fig. 1. Compounds in defensive secretion of *Adelium percatum* and *A. pustolosum*. *a;* 2-methyl-1,4-benzoquinone; *b;* 2,3-dimethyl-1,4-benzoquinone; *c;* 1-pentadecene.

property of tanning human skin. Our fingertips were always darkly mottled after handling a quantity of the beetles.

Secretion for analysis was obtained by seizing and squeezing individual beetles in forceps and wiping the fluid from the everted glands with small pieces of filter paper. The chemical procedure and the findings were the same for both species. Extraction of the papers with methylene chloride, followed by gas chromatography of the extract (1% OV-1 on Gas Chrom. Q, 4′ × ⅛″, 50° to 240°C), revealed the presence of three major components. Analysis by gas chromatography-mass spectrometry showed two of the components to have mass spectra identical to the published spectra (Budzikiewicz *et al.,* 1967) of 2-methyl-1,4-benzoquinone and 2,3-dimethyl-1,4-benzoquinone (Fig. 1 a, b). The third component had a mass spectrum matching that of 1-pentadecene (Stenhagen *et al.,* 1969) (Fig. 1 c). Definitive confirmation of the position of the double bond in this compound was obtained by ozonolysis. A small sample of the third component was collected from the gas chromatograph and dissolved in methylene chloride, and the cooled solution (−70°C) was subjected to a slow bubbled stream of ozone in oxygen until the blue color persisted. Addition of a small crystal of triphenylphosphine, followed by gas chromatography-mass spectrometry, showed the higher molecular weight product to have a mass spectrum identical to that of tetradecanal (Stenhagen *et al.,* 1969).

One interesting point in connection with these analyses was the observation of a fourth component in the initial sample of secretion obtained from both species. This component was guessed to be 1,2-dichloropentadecane on the basis of its mass spectrum, and the identification was confirmed by direct comparison of the isolated material with an authentic sample prepared by addition of chlorine to 1-pentadecene. However, since additional milkings taken from the same

beetles four months later into carbon disulfide rather than methylene chloride failed to show this component, it is apparent that the dihalide is an artifact derived from the olefin.

Structure and Defensive Operation of the Glands

Although the two beetles differ slightly in size and appearance — *A. percatum* is less rotund and longer (1.5-1.9 cm) than *A. pustulosum* (1.3-1.5 cm) — their glandular apparatuses are essentially identical. No dissections of fresh beetles were made, but judging from what could be discerned from specimens somewhat inadequately preserved in ethanol, the glands are anatomically similar in both species and probably homologous to eversible glands such as have been described for other tenebrionids (Lengerken, 1925; Roth, 1945; Tschinkel, 1972). Such glands are basically cuticular sacs, ordinarily withheld in inverted condition within the body cavity, and presumably everted by blood pressure. What is unusual about the *Adelium* glands is that they extrude to such great lengths. For example, gland length in a specimen of *A. percatum* 1.8 cm long that was freeze-dried with its glands everted, was recorded at 0.8 cm. Relative to body size, the glands of these beetles must rate among the largest eversible glands known for insects.

Examination of a glandular sac of *A. percatum,* treated with warm aqueous potassium hydroxide to remove all soft cellular parts, revealed a conventional membranous cuticular lining, with typical cuticular organelles attached (Fig. 8). Such organelles are a diagnostic feature of many insect gland cells (references in Eisner, 1970), and the ones of *Adelium* resemble closely those described from *cell type 1* in the defensive gland of the tenebrionid *Eleodes longicollis* (Eisner *et al.,* 1964). The organelles were distributed along the full length of the glandular sac, indicating that the secretory tissue is not restricted to a limited portion of the gland.

Gentle handling of *Adelium* usually induced no gland eversion at all. Only when the animals were more forcibly stimulated, as when they were grasped by the body or an appendage and squeezed, did

Figure 2. Pasture land near Gudgenby, A. C. T., Australia, where both species of *Adelium* were taken. Figs. 3-4. *Adelium percatum* responding to pinching of individual hindlegs by everting the gland of the side stimulated. Figs. 5-6. *A. percatum* responding to pinching of left midlegs. In Fig. 5 the gland has been maximally everted and has come into contact with the leg stimulated. In Fig. 6 the gland, on eversion, discharged part of its content as an anteriorly-directed spray (reference bar = 5mm).


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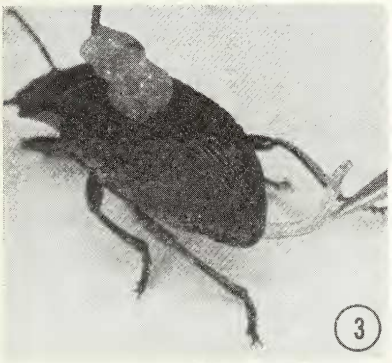
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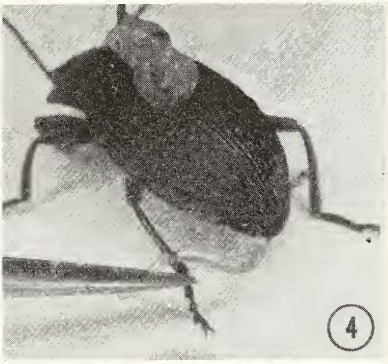
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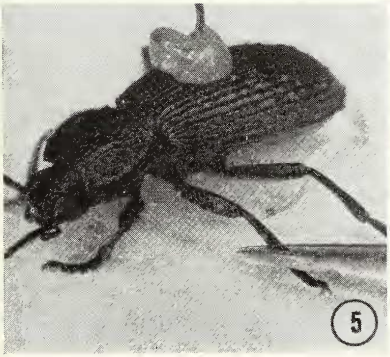
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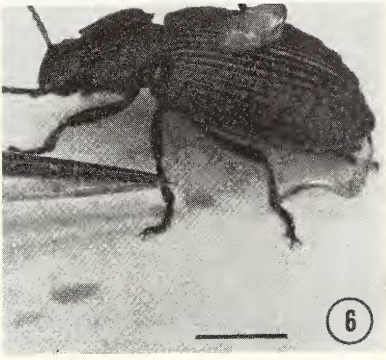
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eversion occur with some consistency. Reluctance to employ the glands in these animals is undoubtedly related to their possession of a particularly tough integument, which may in itself provide an effective first line of defense.

In order to observe more precisely the method of employ of the glands, individual *A. percatum* were affixed to wire tethers with wax, and stimulated by pinching their legs with forceps. The beetles were sometimes placed over filter paper impregnated with an acidified aqueous solution of potassium iodide and starch, a mixture that discolors darkly on exposure to benzoquinones (Roth, 1943) and provides a good visual means for detecting secretory emissions. The results were identical with all nine specimens tested. Stimulation of a single leg generally caused extrusion of only the gland of the corresponding side (Figs. 3-6). Simultaneous stimulation of two legs caused bilateral eversion. The extent and rapidity of extrusion varied, and seemed to depend on the intensity of stimulation. A brief squeeze of a hindleg or midleg, for example, usually induced only a partial eversion of the ipsilateral gland. Protracted or more vigorous squeezing elicited more complete and usually sustained eversion, and the extruded gland commonly extended outward far enough to contact the seized leg or forceps (Figs. 3-5). The target was usually visibly wetted by the gland. The beetles can apparently exercise some control over the direction of extrusion. Thus, when distal parts of a hindleg were stimulated, the gland usually extended outward at a greater angle relative to body axis than when more proximal parts of the leg were grasped. The gland is apparently aimed by flexion at its base rather than along its length, as evidenced by the fact that its shape is relatively fixed irrespective of its angle of protrusion.

When gland eversion occurred abruptly rather than gradually, as was generally the case in response to vigorous pinching, the sudden extension of the gland sometimes caused secretion to be ejected forcibly as a spray. (Figs. 6, 7). Ejections ranged from 1 to 5 cm, but in one instance droplets were shot to as far as 25 cm from the beetle. Forelegs and such other parts on the front of a beetle as are ordinarily inaccessible to the glands were inevitably doused by such ejections. Only beetles with replete or nearly replete glands tended to spray. However, animals with partly depleted glands could still effectively administer secretion to their front end. They did this by relaying secretion from one pair of legs to another, following initial wetting of the hindlegs by the glands. Even the antennae and the head itself were eventually wetted with secretion if they had been

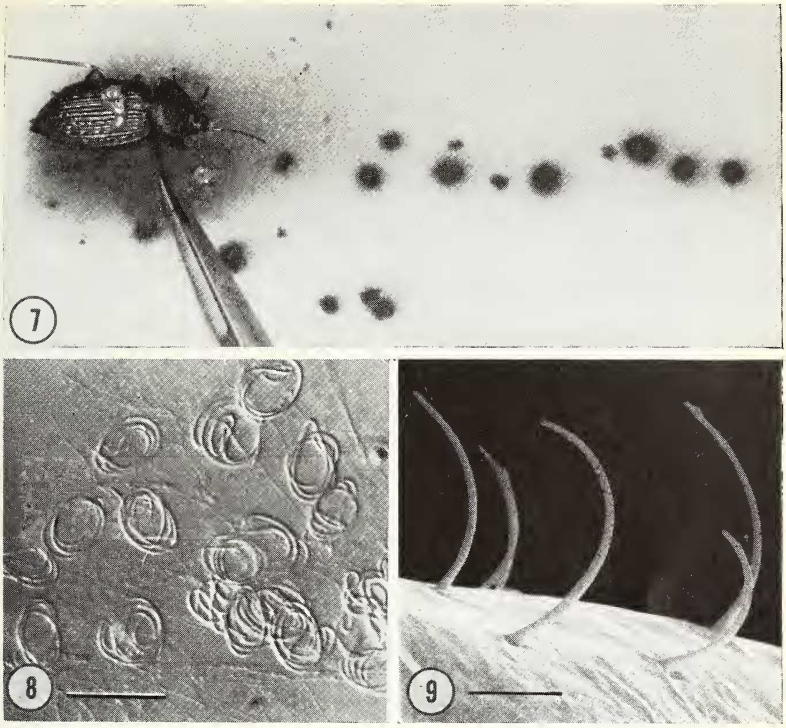


Fig. 7. Response of *Adelium percatum* to pinching of its right midleg. The animal everted its right gland abruptly, causing secretion to be sprayed forward. The droplets of secretion are shown as black spots on the indicator paper that served as substrate (filter paper impregnated with acidified aqueous solution of potassium iodide and starch). Far-ranging discharges as shown here occurred only when beetles had fully replete glands. Fig. 8. Cuticular organelles from secretory cells of gland of *A. percatum,* isolated by treatment of gland with warm 10% aqueous potassium hydroxide (Nomarski interference contrast; reference bar = 30μ). Fig. 9. Scanning electronmicrograph of hairs on exposed surface of everted gland of *A. percatum* (reference bar = 5μ).

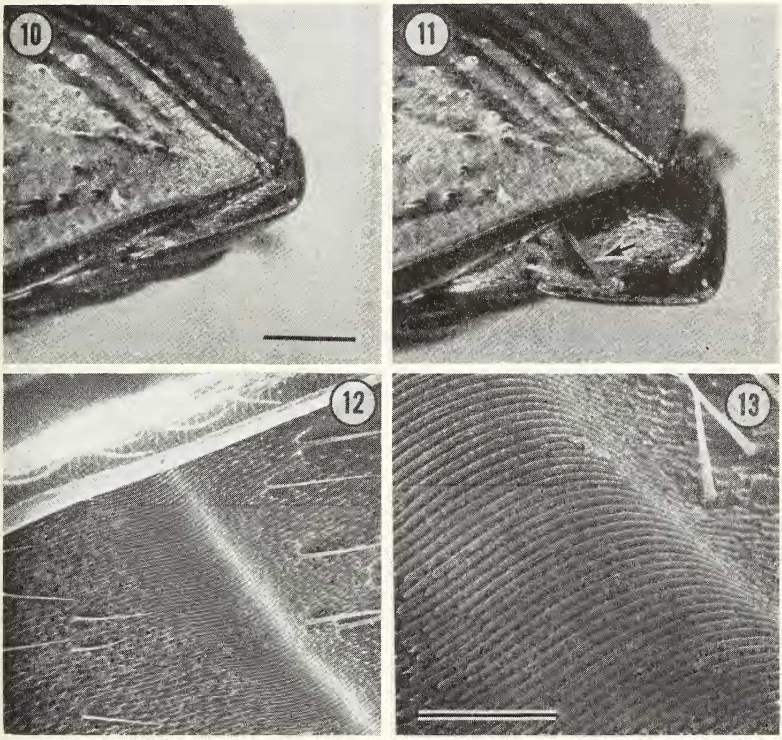
seized in forceps. The initial contact of hindlegs and glands appeared at times to be deliberate rather than fortuitous. Thus, when glands were insufficiently everted to effect automatic contact with the hindlegs, the legs sometimes reached back toward the glands and brushed against them. Wiping of midlegs against hindlegs, and of forelegs against midlegs, quickly followed. In cases where the beetles had been placed on indicator paper, the legs left dark markings on the substrate as evidence of their contamination. Some experiments comparable to the preceding were also done with *A. pustulosum,* with essentially similar results. However, forcible gland eversion with spray ejection was never seen in this species.

Scanning electronmicroscopic examination of the surface of everted glands of *A. percatum* revealed a covering of slender curved hairs (Fig. 9). Whether these are spaced closely enough to act as a matting remains uncertain. But it is conceivable that they function in this capacity, providing perhaps for the maintenance of uniform secretory wetness over the surface of the glands when they are everted and for spontaneous re-spreading of secretion over areas wiped clean by defensive action of the glands. Dispensation of secretion onto target surfaces might also be facilitated by the hairs.

Stridulatory Mechanism

When seized or pinched, *A. pustulosum* produced a distinctly audible sound. The response took precedence over gland eversion, and could persist for seconds if the disturbance was sustained. Two serrate ridges on the last (visible) abdominal tergite (Figs. 10-13) are responsible for engendering the sound. By rhythmic downward deflection of the abdominal tip — a motion depicted in Figs. 10 and 11 — the beetles scrape the ridges back and forth across the sharp overhanging elytral margins, thereby inducing a repetitive bi-syllabic chirp. Intensified stimulation eventually caused gland extrusion, which silenced the sound, since during gland eversion abdominal deflection is apparently precluded. *A. percatum* lacks the ridges and is soundless.

Stridulatory mechanisms are common in insects, and have been repeatedly noted. In the leaf-cutting ant, *Atta cehpalotes,* which produces sound by scraping a file in much the same manner as does *Adelium,* acoustical output and sound generation have been masterfully analyzed (Markl, 1968). Since this analysis is essentially applicable to *Adelium,* we will here describe only the properties of



Figs. 10-11. Dorsolateral view of rear of body of *Adelium pustulosum*, showing the abdominal tip in the undeflected (Fig. 10) and deflected (Fig. 11) positions that mark the limits of the stridulatory motion. The arrow points toward the left serrated ridge (reference bar = 1 mm). Figs. 12-13. Scanning electronmicrographs of the left stridulatory ridge. The elytral margin against which the ridge is scraped extends across the top of Fig. 12 (reference bar Fig. 13 = .05 mm).

the beetle's sound, without detailed consideration of the physical basis of sound production.

Only two live females and one male of *A. pustulosum* were available for sound studies. The animals were affixed to wire tethers glued to their pronotum with wax, and induced to stridulate by pinching their legs individually with forceps. Sound recordings were made with the beetles held at 1 cm from the microphone. An oscillogram of a typical chirp sequence is shown in Fig. 14A. The bi-syllabic composition of each chirp, indicative of the bi-directional movement of the ridges across the elytral margins, is clearly evident. Measurements made from oscillograms, of chirp repetition rates, chirp and syllable durations, and duration of inter-chirp and inter-syllable intervals, are summarized in Table 1, together with measurements of tooth counts and tooth spacings made from the serrate ridges. These parameters are evidently remarkably constant for any one beetle, although they differ somewhat between beetles. The Table does not give an indication of the gradual decline in the chirp repetition rate that characteristically took place with time following onset of pinching of a given leg (e.g. in a female, the rate declined from 2.25 to 1.63 chirps/sec over a period of 4.5 seconds). The decline occurred by a lengthening of the inter-chirp interval, rather than by prolongation of the syllables or inter-syllabic interval of the chirp itself. Accelerated chirping (or gland eversion) always occurred when pinching was shifted to a new leg or increased in intensity.

As was to be expected by analogy with the stridulatory chirps of *Atta,* and shown clearly by the oscillograms (Fig. 14B, C), the syllables are essentially trains of sound pulses, generated by impact of the elytral margins with the sequence of teeth on the ridges. Figs. 14D and 14E show oscillograms of individual pulses from a first and second syllable respectively.

Spectrograph analysis (Fig. 15) of the chirps revealed a frequency composition ranging broadly from below 1 kHz to 60 kHz. The frenquency distribution pattern was essentially similar in the first and second syllables, and differed little in spectrographs made with broad-band (Fig. 15 top) and narrow-band (Fig. 15 bottom) filters. Since broad-band filtration essentially analyzed the pulses one at a time, rather than in groups of three to five as in narrow-band filtration, it follows that the pulses themselves contain essentially the full range of the beetle's sound frequencies.

Apparatus for measuring sound intensities became available only after the beetles had died. Intensities therefore had to be measured

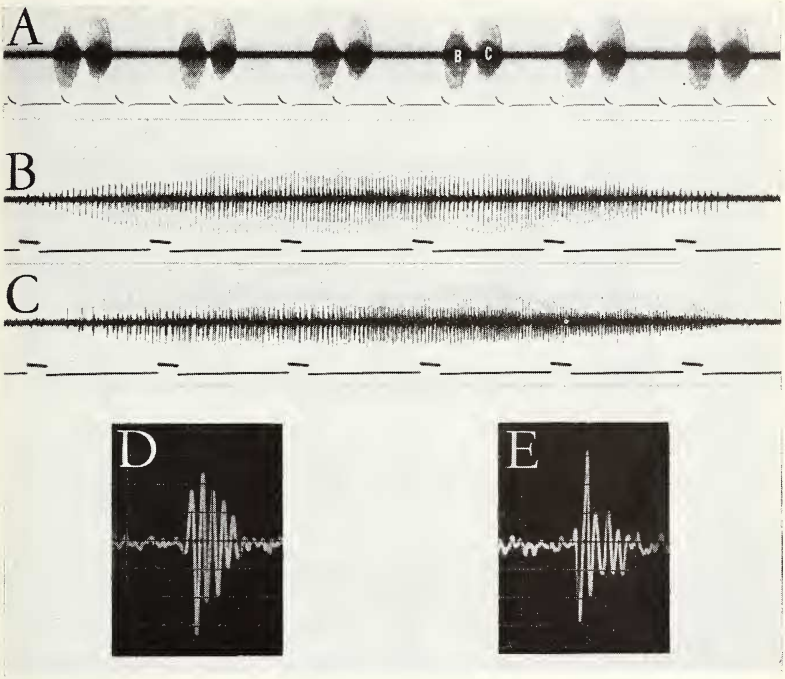


Fig. 14. Sound oscillograms of *Adelium pustulosum*. *A*, chirp sequence (2.8 sec. of ♀ no. 1); note bisyllabic composition of chirps (time interval = 200 msec). *B-C*, Expansion of the first (*B*) and second (*C*) syllables of chirp shown lettered in *A*; the pulsed nature of the sound is clearly resolved (time interval = 20 msec). *D-E*, Individual pulses of first (*D*) and second (*E*) syllables. (0.0625 msec/division).

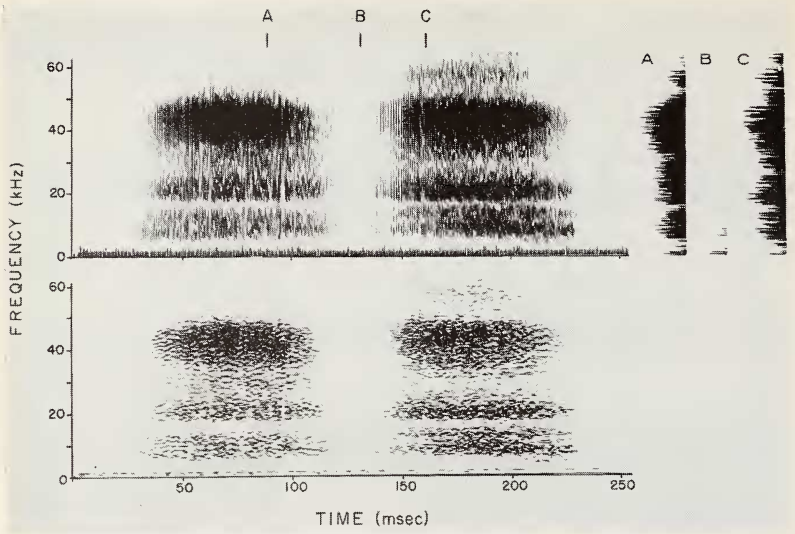


Fig. 15. Sound spectrograms of one chirp of *Adelium pustulosum* (the chirp is that lettered *BC* in Fig. 14*A*, and shown expanded in Fig. 14*B* and *C*). In each spectrogram the first syllable is on left and second syllable on right. Spectrograms were made from recorded sounds replayed at 1/8 speed. Top spectrogram: wide band analyzing filter (effective bandwidth 2400 Hz, with effective time response of 0.375 msec); bottom spectrogram: narrow band analyzing filter (effective bandwidth 360 Hz, with effective time response of 2.75 msec). Beside the top spectrogram are shown energy distribution profiles, corresponding to time transects lettered on the spectrogram itself.

indirectly, from the tape-recorded sounds of the beetles. This was done by monitoring the playback of the recordings with a microphone pickup and oscilloscope (the same microphone as used previously for recording of the chirps), and adusting the intensity of the playback until the induced oscilloscope signal matched that initially elicited by live beetles held 1 cm from the microphone. The intensity of the adjusted playback was then measured with the Sound Level Meter positioned at the site of the microphone, and found to be 65 db (relative to 0.0002 dynes/cm^2).

Detailed analysis of the oscillograms showed that the beetles apparently do not scrape both ridges with equal consistency during stridulation. In fact, stridulation appears to involve predominant scraping of only one ridge during downward deflection of the ab-

dominal tip (first syllable), and of both ridges with somewhat unequal force during the upward movement of the tip (second syllable). This conclusion rests on the observation that the syllables contain, in addition to a consistent major pulse (which in total number per syllable corresponds to the number of teeth per length of file estimated to be scraped during a syllable)[1], a subsidiary pulse of varying lesser amplitude, which appears sporadically in the first syllable, and fairly consistently in the second syllable. These lesser pulses, when they appear, result in a doubling of the pulse repetition rate. Moreover they bear a shifting rather than fixed temporal relationship to the primary pulses, suggesting that they are not subsidiary acoustical concomitants of single tooth scrapings, but a consequence of scraping of a second set of teeth of somewhat unmatched spacing relative to the first. The near absence of secondary pulses in the first syllable suggests that the beetle might not press the abdominal tip as vigorously against the elytral margins during downward abdominal deflection as during the return motion.

Discussion

Defensive glands that produce quinones are widespread among arthropods. They have been reported not only from other Tenebrionidae (references in Jacobson, 1966; Roth and Eisner, 1962; Weatherston, 1967; Weatherston and Percy, 1970), but also from certain termites (Moore, 1968), earwigs (Eisner and Blumberg, 1959; Schildknecht and Weis, 1960), cockroaches (Roth and Stay, 1958), grasshoppers (Eisner *et al.*, 1971a), carabid beetles (Aneshansley *et al.*, 1969; references in Moore and Wallbank, 1968; Schildknecht *et al.*, 1968), staphylinid beetles (Blum *et al.*, 1971; Brand *et al.*, 1973), millipedes (references in Jacobson, 1966; Roth and Eisner, 1962; Weatherston, 1967; Weatherston and Percy, 1970) and opilionids (Fieser and Ardao, 1956; Eisner *et al.*, 1971b). As is often the case with arthropod defenses, they exist as close counterparts in plants: glandular hairs that secrete a benzoquinone have been described for *Primula obconica* (Schildknecht *et al.*, 1967). Contrary to claim (Schildknecht *et al.*, 1964), not all Tenebrionidae

[1]From photographs such as Figs. 10 and 11, which depict the motion of the abdominal tip during chirping, it was estimated that this motion has a maximum amplitude of *ca.* 2/3 the length of a serrated ridge. This corresponds to about 130 teeth, a figure in line with the counted maxima of major pulses in the syllables.

have defensive glands (e.g., Tentyriinae and Asidinae). But the glands are frequently present, and when they are, they are either exclusively abdominal as in *Adelium,* or supplemented by a second pair of glands in the prothorax (Roth, 1945; Tschinkel, 1969).

Only relatively few tenebrionid secretions have been studied chemically. Most produce benzoquinones, including *p*-benzoquinone, and its alkylated derivatives 2-methyl-1,4-benzoquinone and 2-ethyl-1,4-benzoquinone (references in Jacobson, 1966; Roth and Eisner, 1962; Weatherston, 1967; Weatherston and Percy, 1970). Naphthoquinones have been reported in one species (Tschinkel, 1972) and in another the prothoracic glands produce phenols instead of quinones (Tschinkel, 1969). 2,3-Dimethyl-1,4-benzoquinone itself has not been found in a tenebrionid secretion, but it is produced by the defensive glands of certain opilionids (Fieser and Ardao, 1956; Eisner *et al.,* 1971b). The presence of an alkene in *Adelium* is no novelty. Hydrocarbons, both saturated and unsaturated, are known from arthropod secretions, and although 1-pentadecene as such has not been reported, shorter chain homologs of the substance are present in Tenebrionidae (Hurst *et al.,* 1964).

We made no effort to evaluate the defensive effectiveness of the secretion of *Adelium.* However, judging from the proven deterrency of other quinonoid mixtures to predators (references in Eisner, 1970, 1972; Eisner and Meinwald 1966), there can be no doubt that the glands of *Adelium* are protective in function. The presence of the alkene may be of more than incidental significance. It has been argued (Blum and Crain, 1961), and in one case proven (Eisner *et al.,* 1961), that lipoidal additives promote spreading and penetration of defensive secretions on target.

Defensive glands of arthropods vary greatly in structure and operation, and several characteristic types have been recognized (Eisner, 1970). The glands of *Adelium* appear to combine features of two of these types. Basically, by virtue of their extrusibility, they clasify as conventional *eversible* glands, but since they occasionally eject their

Table 1. *Adelium pustulosum:* Temporal characteristics of the chirps and morphological features of the stridulatory ridges. Temporal measurements were made from oscillograms and are given as mean ± standard error; sample size (N) is given in parenthesis. Morphological measurements were made from microscopic preparations of the last abdominal tergite of the beetles; tooth spacing was calculated by dividing ridge length by tooth number. (The tergite of ♀ no. 1 was damaged in preparation, hence the omission of measurements from one ridge.)

Table 1

Beetle No.	Chirp Rate (chirps/sec)	Duration (msec) of:				
		Entire Chirp	Interchirp Interval	1st Syllable	2nd Syllable	Intersyllabic Interval
1 ♀	1.96 ± 0.07 (15)	219.9 ± 3.9 (16)	290.0 ± 17.5 (15)	102.6 ± 1.4 (16)	97.6 ± 3.1 (16)	19.6 ± 1.1 (16)
2 ♀	2.26 ± 0.05 (26)	276.6 ± 6.1 (31)	161.0 ± 12.6 (26)	82.4 ± 3.4 (31)	123.4 ± 4.4 (31)	71.2 ± 4.0 (31)
3 ♂	2.66 ± 0.10 (26)	274.9 ± 4.8 (27)	99.4 ± 11.7 (26)	119.7 ± 2.6 (27)	130.0 ± 3.7 (27)	25.3 ± 0.8 (27)

Beetle No.	No. and Spacing (μ) of Teeth of Left (L) and Right (R) ridges			
	No. (L)	Spacing (L)	No. (R)	Spacing (R)
1 ♀	—	—	205	3.8
2 ♀	195	3.8	185	4.0
3 ♂	190	3.8	180	3.9

contents, they also qualify as *spraying* glands. We know of no other tenebrionid glands that operate in this way. Eversible glands are common, but they are generally shorter than those of *Adelium* and do not eject spray on extrusion. Spraying does occur, but only from non-eversible glands, as in *Eleodes* (Eisner, 1966). The peculiar habit of *Adelium* of relaying secretion by way of its appendages is not unique. Other tenebrionids are also said to use their legs for administration of secretion (Tschinkel, 1972), and comparable behavior has been reported for opilionids (Eisner *et al.*, 1971b) and Hemiptera (Remold, 1962).

Many insects produce chirps or other "disturbance" calls when they are molested. Cerambycid beetles, for example, very generally show this property, as do other beetles, cockroaches, Hemiptera, adult and immature Lepidoptera, and members of most other groups, including non-insectan arthropods (references in Alexander, 1967; Haskell, 1961; Roth and Hartman, 1967; Tuxen, 1967). The sounds are generally believed to be defensive, but it is by no means clear how precisely they act in this capacity. Convincing evidence has been advanced to account for the function of the calls in arctiid moths. These insects are chemically protected (Bisset *et al.*, 1960) and hence presumably distasteful, and they emit sounds, rich in ultrasound, in response to the echolocating chirps of bats (Blest *et al.*, 1963). Bats turn away from the calls, presumably because they have learned on the basis of previous experience with the moths that a prospective meal that "protests" audibly is distasteful (Dunning and Roeder, 1965; Roeder, 1967). The sounds, then, act as acoustical aposematic signals, operative in the dark just as visual aposematic adornments supposedly operate in the light. Defensive calls generally, to the extent that they are produced by chemically or otherwise protected insects and induced by encounters with predators, may function in this way. They might certainly do so in *Adelium pustulosum,* a furtive animal most likely to meet its enemies in darkness. But the calls need not only serve for acoustical reinforcement of a concomitant defense. They could also be intrinsically deterrent to predators, perhaps only to some, or they might function socially — as do "alarm" sounds in termites and ants (Howse, 1964; Markl, 1967, 1969; Markl and Fuchs, 1972) — to alert conspecifics to states of emergency. But these possibilities, like so many other functional suggestions that have been advanced for disturbance calls, remain to be proven. One wonders what predators might be affected by the chirps of *Adelium,* although criteria for compiling a list of enemies are lack-

ing. It seems clear, however, that the chirps are of sufficiently broad frequency composition to be at least potentially audible to virtually any acoustically sensitive predator.

Summary

The black flightless tenebrionid beetles *Adelium percatum* and *A. pustulosum* from Australia possess a pair of eversible abdominal glands that secrete a mixture of 2-methyl-1,4-benzoquinone, 2,3-dimethyl-1,4-benzoquinone, and 1-pentadecene. The tubular glands are unusually large, and when everted may be nearly half as long as the beetles themselves. In *A. percatum,* the replete glands may, on extrusion, spray their contents forcibly, to a recorded maximum distance of 25 cm. Defensive administration of secretion is also effected by the beetles' legs. *A. pustulosum,* unlike *A. percatum,* produces an audible "disturbance sound" when molested. The sound is engendered by the scraping of two serrated ridges on the last abdominal tergum across the elytral margins. The morphology of the stridulatory apparatus, and the acoustical properties of the sound, which contains frequencies ranging from below 1 kHz to 60 kHz, are presented. It is argued that disturbance sounds, when produced by chemically or otherwise protected animals, act as acoustical aposematic signals, operative primarily in darkness.

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